

## Differential survival rates of damselfly larvae in the presence of newt and dragonfly predators

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The damselfly species *Paracercion melanotum* has been found to be the most abundant species in damselfly larval communities on Okinawa-zima Island in southwest Japan. To clarify differential susceptibility to predation, a possible factor affecting relative population densities in larval communities, between *Paracercion melanotum* and a less common damselfly species, *Ischnura senegalensis*, laboratory experiments were conducted using three abundant predator species: the sword-tailed newt (*Cynops ensicauda popei*), anisopteran larvae (*Crocothemis servilia servilia*), and a planktivorous fish (*Poecilia reticulata*). *Paracercion melanotum* survived predation by the newt and the dragonfly well compared to *I. senegalensis*. Fishes consumed approximately equal numbers of the two damselfly species. From these results, the newt and the dragonfly were suggested as the most probable predators regulating damselfly larval communities on Okinawa-zima Island. Predators could be a crucial factor determining relative abundance in damselfly larval communities.

**Keywords:** Anisoptera; damselfly; dragonfly; Odonata; predatory behavior; relative abundance; sword-tailed newt; Zygoptera

### Introduction

Predators can influence prey population densities and relative abundance in a prey community (Arditi & Ginzburg, 1989; Chase & Leibold, 2003). Some prey that are aware of predator scents change their traits to avoid predation (Arnqvist & Johansson, 1998; Kolar & Wahl, 1998; Mikolajewski et al., 2006). A single prey species is often under the influence of various predator species, and should, as much as possible, find ways to avoid predation from diverse predators (Sih et al., 1998). As trade-offs in resource allocation prevent a prey species from evolving perfect defenses against all predators, different prey species have developed different ways to cope with a predator species. Such diverse evolutionary pathways have led to many prey species coexisting in a habitat (Chase & Leibold, 2003).

Damselfly larvae are under strong predation pressure (Johnson, 1991). Among these predators, fishes are an overwhelmingly influential predator group for larval damselfly communities (Corbet, 1999; McPeck, 1998). Insectivorous fishes can eat many individuals, and damselfly larvae are forced out of fish habitats if they do not adapt to fish predators. In habitats without fishes, the

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larvae of dragonflies are often top predators of damselfly larvae, and damselfly larvae that are adapted to fish predators are generally not well adapted to withstand predation pressure from such invertebrate predators (McPeck, 1990). This is because each predator engages in different predatory behaviors to capture their prey, and a strategy to escape from a given predator species generally cannot be used against another predator species. Hence, these variations of predator and prey species determine the patterns of coexistence in habitats.

Six zygopteran species have been recorded on Okinawa-zima Island in the southwest of Japan (Watanabe, Kohama, Yakita, & Ozono, 2007). Larval damselflies in two natural ponds on the island were sampled through 13 consecutive months, and four damselfly species were present constantly throughout the sampling period. Among the four species, *Paracercion melanotum* (Selys, 1876) was always the most abundant species in damselfly communities (Katayama & Tatsuta, 2012). On the island, large predatory fishes are uncommon in natural ponds, except for exotic fishes, which are often found in artificial ponds (Nishijima, 2003). In the two natural ponds, no fish predators were found except for small planktivorous fishes (*Oryzias latipes* and *Xiphophorus helleri*). However, sword-tailed newts (*Cynops ensicauda popei*) and larvae of anisopteran species were abundant and coexisted with damselfly larvae regardless of season (Katayama, unpublished data). This suggests that *P. melanotum* could cope well with these predators in comparison with other, less common, zygopteran species. Laboratory experiments were conducted to reveal whether the susceptibility to predators of *P. melanotum* was low compared to those of less common species. The hypothesis addressed here was that the most abundant *P. melanotum* survived well from these common predators.

## Materials and methods

### Experimental animals

Two damselfly species were chosen for comparison. One was the most abundant *P. melanotum* and the other was a less common species, *Ischnura senegalensis* Rambur (1842), which was the second most abundant species in the two ponds (two other species occurred, *Ceriagrion auranticum ryukyuanum* Asahina and *Agriocnemis femina oryzae* Lieftink) and was also abundant in ephemeral and artificial environments. *Paracercion melanotum* (mean body length without caudal lamellae  $\pm$  SD: 11.75  $\pm$  3.32 mm) was collected from a natural pond (26°4'59" N, 128°8'54" E) and *I. senegalensis* (mean body length without caudal lamellae  $\pm$  SD : 10.55  $\pm$  1.89 mm) was collected from an irrigation ditch (26°9'27" N, 127°46'37" E). Each individual was kept in a plastic vial (30  $\times$  115 mm) separately with a wood perch and fed newly hatched brine shrimps (*Artemia salina*) *ad libitum*.

Three predator species were considered: the newt, a dragonfly, and a fish. Nine male (mean snout-to-vent length (SVL)  $\pm$  SD: 5.84  $\pm$  0.32 cm) and nine female (mean SVL  $\pm$  SD: 6.34  $\pm$  0.26 cm) newts were collected from a natural pond at Nanzyô City, and kept in plastic cases separately with water (25  $\times$  15  $\times$  15 cm; 10 cm water depth), and fed commercially available turtle food *ad libitum*. The larva of an anisopteran species (*Crocothemis servilia servilia*) was one of the most abundant dragonfly species in the two ponds and was selected as the dragonfly predator. Forty-eight larvae (mean head width  $\pm$  SD: 5.49  $\pm$  0.54 mm) were collected from a natural pond and kept in a tank (450  $\times$  300  $\times$  300 mm) with many macrophyte stems as perches. Guppies (*Poecilia reticulata*) were chosen as the fish predator because they are mainly planktivorous and somewhat resemble the two coexisting fishes from the two ponds. They have naturalized on the island and were easily available. Forty-two fishes (mean body length  $\pm$  SD: 24.14  $\pm$  1.93 mm) were caught from an artificial pond in Nisihara Town and kept in a tank (450  $\times$  300  $\times$  300 mm)

with many macrophyte stems. All animals were caught in February 2010, and kept under laboratory conditions (12 h L/ 12 h D., 25°C).

### **Experimental protocol**

Plastic tanks (300 × 195 × 205 mm) were used for all experiments. The bottom of each tank was covered with commercially available gardening soil to a thickness of 3 cm. Tanks, filled with water to a height of 15 cm from the bottom, were acclimatized to the laboratory conditions for 24 h prior to the start of trials. After this period, tanks were separated in half by a plastic plate. Three larvae of each damselfly species (i.e. six larvae in total) were randomly selected and placed into one side of the separated tank, while a predator was placed the other side of the tank. Half an hour was allowed for animals to acclimate to the experimental conditions. Then, the plastic plate was removed and the trial started. One newt was used for each trial, while three individuals of the dragonfly and the fishes were used for each trial based on their capacity to prey on the damselfly larvae. Each trial ran for 12 h with 6 light and 6 dark hours. After a trial, surviving larvae were counted. Trials without any predators were used as controls.

The newt experiments were conducted on two consecutive days, half with male and half with female newts on each day. The other three treatments needed three days, which consisted of one treatment per day. In total, these experiments finished in five days.

### **Statistical analysis**

Generalized linear models were used to assess differences in the survival rates of the two damselfly species. For the newt experiments ( $n = 18$ ), a binomial error distribution (logit link function) was assumed and the function “glm” was used. As datasets were over-dispersed in both the dragonfly ( $n = 16$ ) and fish experiments ( $n = 14$ ) when binomial error distributions were assumed, each plastic case was treated as a random factor to mitigate for the over-dispersed datasets. Hence, for these two predators, the function “glmmML” in the glmmML library was used. The Akaike information criterion (AIC) was calculated for each model, and all models were ranked in ascending order based on the AIC value (Anderson et al., 2000; Burnham & Anderson, 2002). The model with the lowest value would be recognized as the best model. Akaike weights were also calculated for each model, to represent the relative likelihood of each model among the candidate models. Since each model of the newt trials had some support, based on their relative likelihoods (see “Results”), model-averaged estimated coefficients are presented in the “Results” section (Burnham & Anderson, 2002; see Table 2).

## **Results**

In the without-predator control treatment, almost all larvae were alive after the experimental period (Figure 1a). In the newt trials, males consumed more larvae than females during the experimental period. *Ischnura senegalensis* was more susceptible to newt predation than *P. melanotum* regardless of newt sex (Figure 1b). The best model of the newt trials contained two main factors, damselfly species and sex, which accounted for almost half of the relative likelihood (Table 1). The second model contained only sex as a factor. The average variable coefficients showed that *P. melanotum* had higher survival rates than *I. senegalensis*, and the survival rates of the two species decreased equally when they suffered from male predation pressure, because the interaction term was small (Tables 1 and 2). Similarly, *I. senegalensis* was more susceptible to dragonfly predation than *P. melanotum* (Figure 1c). The best model, which had a quite high likelihood,

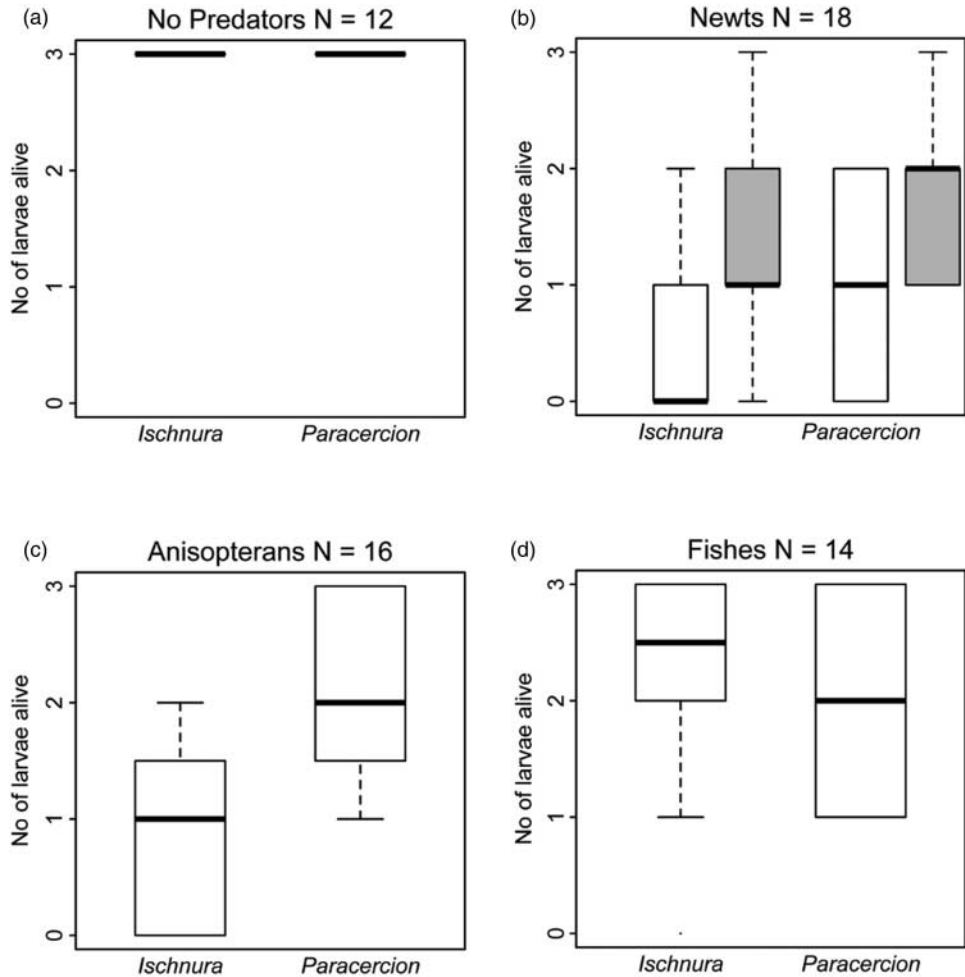


Figure 1. Box plots of the number of larvae alive after the experimental period. The bold line near the middle of the box represents the median value. The bottom and the top of the box represent the lower quartile and the upper quartile respectively (25th and 75th percentile). In newts, white and gray bars indicate male and female newts respectively. (a) No predators control, (b) newt predators, (c) dragonfly predators, and (d) fish predators.

contained damselfly species as the main factor (Table 1). Estimated coefficients confirmed the higher survival rates of *P. melanotum* (Table 2). In contrast, *I. senegalensis* was somewhat less susceptible than *P. melanotum* to fish predators (Figure 1d). However, the best model of the fish trials was the null model, which contained only the intercept term, and the support for these models was weak (Tables 1, 2).

### Discussion

This study showed that the most abundant damselfly species, *Paracercion melanotum*, was less susceptible to predators than the less common species, *Ischnura senegalensis*. The sword-tailed newt and dragonfly larva were the most influential predators, with little effect by the fish, which was mainly planktivorous. The results suggest that predators' effects are an important factor regulating the relative abundance in damselfly communities on Okinawa-zima Island.

Table 1. Statistics calculated for each model. The model order was based on their AIC values.

Variable	AIC	$\Delta$ AIC	wi
<i>Newt</i>			
Damselfly + sex	86.8		0.482
Sex	87.7	0.83	0.319
Damselfly + sex + damselfly $\times$ sex	88.7	1.89	0.187
Damselfly	95.5	8.65	0.006
Null	96	9.21	0.005
<i>Dragonfly</i>			
Damselfly	43.4		0.999
Null	56.8	13.47	0.001
<i>Fish</i>			
Null	41.3	0	0.535
Damselfly	41.6	0.28	0.465

Note: AIC: Akaike information criterion,  $\Delta$ AIC: the difference in AIC values between the best and focal model, wi: Akaike weights.

Table 2. Estimated coefficients of each variable.

Variables	Estimate	SE
<i>Newts</i>		
Intercept	−0.16	0.31
Paracercion	0.46	0.23
Male	−1.36	0.39
Paracercion $\times$ male	0.053	0.086
<i>Anisopterans</i>		
Intercept	−0.79	0.31
Paracercion	1.68	0.44
<i>Fishes</i>		
Intercept	1.42	0.51
Paracercion	−0.70	0.54

Note: Intercept represents the value of *I. senegalensis*.

Predators affect the spatial distributions of Odonata larvae. Two species of *Enallagma*, showing non-overlapping spatial distributions among ponds, differ in their susceptibility to predation (Pierce & Crowley, 1985). Larvae of *Enallagma aspersum* were more active than those of *E. traviatum*, and active *E. aspersum* were more susceptible to predation when faced with fish predators. In contrast, less active *E. traviatum* were eaten more easily by large Odonata species such as *Aeshna*, which is a top predator in ponds without fish predators (Corbet, 1999). Odonata predators easily capture and eat less active damselfly larvae, whereas fishes tend to eat active larvae (McPeck, 1990; McPeck et al., 2001). On Okinawa-zima Island, native fishes living in ponds are often planktivorous (Nishijima, 2003). Guppies, which resemble the native *Oryzias latipes* in body size and food habits, did not eat very many damselflies and were the weakest of the three predators used in the experiment. However, the sword-tailed newts and dragonfly larvae ate fewer *P. melanotum* larvae than *I. senegalensis*. The newt is widely distributed and common in moist forests on the island (Katayama, 2011; Tominaga et al., 2010). The dragonfly is also distributed throughout the island (Watanabe et al., 2007). Consequently, a habitat gradient of predator regimes would be difficult to maintain within the confines of the island, unlike in continental regions (Katayama, personal observation). Predators may be a factor affecting the relative abundance in damselfly communities, especially in natural ponds that contain these common predators on Okinawa-zima Island.

Other mechanisms also affect larval damselfly communities. Competition among larvae is often mentioned as such a factor (Corbet, 1999). The ability to use resources correlates with the ability to coexist with predators, and these abilities are often traded off against each other (Chase & Leibold, 2003; McPeck, 1998). Species without adaptations against predators can utilize food more effectively than species with such adaptations. Adult *I. senegalensis* have a high ability to fly long distances, and their larvae are often found even in small and ephemeral water bodies, including artificial environments (Watanabe et al., 2007; Katayama, personal observation). *Ischnura senegalensis* might employ an r-strategy life history, which includes higher dispersal rates, effective use of resources, and rapid growth (Begon et al., 2006; McPeck, 1989).

In conclusion, predator susceptibility of damselfly larvae was negatively correlated with the relative abundance in field communities. As suggested in many studies, predators could have great impacts on damselfly community compositions. However, because this study was conducted only in the laboratory, field manipulations would be needed to further clarify the importance of predators influencing larval damselfly communities.

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